Scientific Papers

Natural History Museum
The University of Kansas

22 December 2008 Number 41:1–19

Male Genitalic Morphology of Orchid Bees of the Genus *Euglossa* (Hymenoptera: Apidae)

By

Ismael A. Hinojosa-Díaz

Division of Entomology, Natural History Museum and Biodiversity Research Center, The University of Kansas, 1501 Crestline Drive – Suite 140, Lawrence Kansas 66045–2811, U.S.A.

CONTENTS

ABSTRACT Orchid bees constitute an interesting group within the corbiculate clade, most noticeable for their appealing external features that are the basis for their classification, with almost no attention given to the diversity of male genital structures. The genus *Euglossa* in particular has suffered a paucity of information about male genital structures, which offer substantial information to solve some controversial taxonomic positions and add numerous characters for phylogenetic studies. The present work presents a detailed description of the genital capsule and associated sterna of *Euglossa imperialis* Cockerell with comparative comments on other *Euglossa* and Euglossini, as well as other corbiculate tribes and some closely related apine lineages. This study is the basis for an ongoing phylogenetic analysis of *Euglossa*, while it is also hoped that it will encourage the use of these structures in comparative work on this notable group of bees.

Key Words: *Euglossa*; Euglossini; Apoidea; corbiculate bees; genitalia; hidden sterna; comparative morphology.

 ISSN No. 1094-0782

RESUMEN Las abejas de las orquídeas sobresalen dentro del grupo de las abejas con corbícula por sus características externas llamativas las cuales han servido de base para su clasificación con nula atención hacia las estructuras genitales de los machos. Esto último con particular énfasis en el género *Euglossa*, para el cual las estructuras genitales ofrecen información sustancial para resolver posiciones taxonómicas controvertidas, al tiempo que constituyen una importante fuente de caracteres de interés en estudios filogenéticos. En este trabajo se presenta una descripción detallada de la cápsula genital y esternos asociados de *Euglossa imperialis* Cockerell con comentarios comparativos para otras especies de *Euglossa* y Euglossini, así como otras tribus de abejas con corbícula y otros linajes de abejas emparentados. Este trabajo es la base de un estudio filogenético en curso de *Euglossa*, además tiene la intención de estimular el uso de las estructuras aquí descritas en estudios comparativos de este atractivo grupo de abejas.

PALABRAS CLAVES: *Euglossa*; Euglossini; Apoidea; abejas con corbícula; genitalia; esternos ocultos; morfología comparada.

INTRODUCTION

The tribe Euglossini encompasses one of the most remarkable groups of bees, outstanding for their biology, their morphological peculiarities, and their phylogenetic position. The striking metallic integumental coloration of most species, particularly of those in the genus *Euglossa* Latreille, makes them hard to pass by. Their common name "orchid bees" derives from the association between male euglossines and orchids, in which males visit orchid flowers in their quest for volatile chemicals offered by the plant as reward in exchange for the pollination services provided (Dressler, 1982a). This peculiar behavior is accompanied by a suite of interesting external morphological features, most of them linked to the gathering, handling, and storing of the chemicals. Species of the genus *Euglossa* exhibit, besides the aforementioned male secondary sexual characteristics, variation in other external features in both sexes, notably, besides the metallic coloration, the length of the labiomaxillary complex from which the genus derives its name (*Euglossa*; Gr. *eu* = true, *glossa* = tongue). Not surprisingly, taxonomic work on this genus has relied heavily on these noteworthy external characteristics, giving almost no attention to the genital structures. With few exceptions (Dressler, 1978a; Parra-H *et al.*, 2006; Ramírez, 2006; Rasmussen and Skov, 2006; Hinojosa-Díaz and Engel, 2007), the vast majority of the little more than 100 species of *Euglossa* (Ramírez *et al.*, 2002; Roubik and Hanson, 2004) have been described without written or graphic reference to the male genital capsule or its associated hidden sterna, in spite of the known importance of these structures in studies of related groups of bees. Likewise, Cockerell (1917), Moure (1967, 1989), and Dressler (1978b, 1982b, c) established the current subgeneric classification based solely on external morphology. In a recent attempt to draw attention to male genital characters for *Euglossa*, Ospina-Torres *et al.* (2006) presented a short review of the variation of gonostylar morphology within the genus. The systematic and phylogenetic value of characters from the male genital capsule and hidden sterna in the tribe Euglossini has been demonstrated when applied to the whole tribe (Kimsey, 1987; Engel, 1999), as well as in studies of *Eufriesea* Cockerell (Kimsey, 1982), *Eulaema* Lepeletier de Saint Fargaeu (Oliveira, 2006) and *Exaerete* Hoffmannsegg (Kimsey, 1979; Anjos-Silva *et al.*, 2007). In *Euglossa*, a recent revision of a section of *Euglossa sensu stricto* (Bembé, 2007), has also demonstrated the utility of this kind of information. The present work presents a detailed review of the male genitalic morphology of the genus *Euglossa* with standardized terminology that will be applied in a phylogenetic study of the genus currently in progress and that could serve as a basis for other studies as well as descriptions of new species.

ACKNOWLEDGMENTS

This paper is part of the doctoral research of the author, most of which has been carried out under the sponsorship of CONACYT (Consejo Nacional de Ciencia y Tecnología, México). Partial support was provided by National Science Foundation grant EF-0341724 (to M.S. Engel). Michael S. Engel provided invaluable help for the development of this work. Dr. Charles D. Michener provided useful comments for every aspect of this work which is dedicated to him in celebration of his 90th birthday this year (22 September 2008). Jerome G. Rozen, Jr., and an anonymous reviewer made valuable comments on this work. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

MATERIALS AND METHODS

Male genital capsules and hidden sterna of several specimens of *Euglossa imperialis* Cockerell were examined by dissecting them from specimens deposited in the Division of Entomology, Natural History Museum and Biodiversity Research Center, University of Kansas. The dissections were performed by severing the metasomal tip consisting of terga 7 to 8, sterna 6 to 8 and the genital capsule. The severed sections were cleared in a solution of potassium hydroxide (KOH) at room temperature for periods of 18 to 36 hours depending on the condition of each specimen, and then transferred to water and alcohol to be finally kept in glycerin. Electronic drawings were generated, using a drawing tablet, for the dissected metasomal hidden sterna (7 and 8) and the genital capsule, as observed on an Olympus SZ60 microscope. For comparative purposes dissections were made of representatives of several other species of *Euglossa* and all other euglossine genera, as well as specimens of *Bombus* Latreille, *Centris* Fabricius, *Epicharis* Klug, and *Anthophora* Latreille (Appendix). In addition, available literature on the genital structures for the aforementioned groups, as well as Meliponini, was studied (Appendix). No comparative statement is made with *Apis* Linnaeus since the male genitalia of this genus is highly derived.

COMPARATIVE MORPHOLOGY

Euglossa imperialis Cockerell, 1922

The morphology of the male genitalia and hidden sterna of *Euglossa* is based on that of *E. imperialis*, as this species exhibits one of the widest distributional ranges of all species within the genus, occurring from southern Mexico to Atlantic Southeast Brazil (Ramírez *et al*., 2002; Roubik, 2004; Roubik and Hanson, 2004; Rebêlo, 2001). Moreover it is typically abundant and commonly collected, well represented in collections, thus ideal as a source of specimens for dissection and as a comparative basis for other species.

Terminology applied to the major sclerotic components of bee male genitalia has been rather stable with some variation in terms according to different authors and taxa, especially if compared to the numerous, sometimes confusing, sets of terms for male genitalic structures throughout Hymenoptera as a whole and insects in general. A sample of different terminologies applied to the different parts of bee and Hymenoptera male genitalia is presented in Table 1. The terminology of Michener (1944a) is here preferred, as it is the most commonly used in bee morphology and taxonomy. The terminology used for the hidden sterna associated with the male genitalia has varied depending on the treatment of them as parts of either the abdomen (eighth and ninth abdominal sterna) or the metasoma (seventh and eighth metasomal sterna); the abdominal numbering was initially used as an attempt to present a regular treatment of these segments for comparison with other Hymenoptera (Michener, 1944a, 1956) and other lineages of insects (Michener 1944b), but the metasomal terminology is by far dominant (e.g., Eickwort, 1969; Brooks, 1988; Michener, 2007; Engel, 2007) and will be followed here.

A description of the male hidden metasomal sterna and the different components of the genital capsule of *E. imperialis* is presented here with comments on variation seen in other *Euglossa* as well as other euglossine genera and related apine bees. Comparative statements of subgeneric assemblages within *Euglossa* in this work refer to the names as they are currently used in most new species descriptions and synoptic lists; the monotypic *Dasystilbe* Dressler offers no interpretational problem and will be referred to by mentioning its only member *E. villosa* Moure. *Euglossa s. str.* and *Euglossella* Moure are treated as Dressler stated in his original subgeneric division (1978b). *Glossura* Cockerell and *Glossurella* Dressler are as subsequently diagnosed by Dressler (1982c), while *Glossuropoda* Moure is taken in its original sense. All comparative statements in the following description containing references to "all species" belonging to subgeneric assemblages refer to those species reviewed (Appendix). As a general practice, when necessary, each structure will be subdivided into major recognizable "sections" referred to in accordance with their general anatomical position. The structures will be presented in the following sequence:

Table 1. Different sets of terminology applied to some relevant parts of male genitalia of bees and Hymenoptera. Terms in the same row are equivalent. The specific group of organisms to which every study refers is shown below the author.

Michener (1944) *Bees* (applied in present work)	Ito (1985) *Bombus*	Schulmeister (2001) Lower Hymenoptera	Michener (2007) Bees
Gonobase	Gonobase	Cupula	Gonobase
Gonocoxite	Gonocoxite	Gonostipes	Gonocoxite
Gonostylus	Squama	Harpe	Gonostylus
	Gonostylus		Volsella*
Penis valve	Penis valve	Penisvalva	Penis valve

* The term volsella was applied by Michener (2007) to different structures in different groups of bees, here is shown in the context for Bombini and Euglossini.

seventh metasomal sternum, eighth metasomal sternum, genitalia, gonobase, gonocoxite, gonostylus, aedeagus, penis valve, and penis.

Seventh metasomal sternum.—This is the first of the pair of hidden metasomal sterna associated with the male genitalia (often referred to as S7) and is invaginated into the metasoma together with the eighth metasomal sternum and the genital capsule (hence the name hidden sterna). In *E. imperialis* the seventh metasomal sternum agrees basically with the general description for *Anthophora* given by Michener (1944a). The whole sternum is curved upwards such that the dorsal (inner) surface is concave and the ventral (outer) surface is convex. It has a rather trapezoidal disc continued laterally by the long anterolateral arms (Fig. 1). The anterior edge is strongly concave. The posterior edge of the disc is divided by an acute triangular incision whose depth (length) equals its width and forms an interior angle of around 70°. The lobes of the disc, formed by the incision, are slightly wider than long and are oriented posterolaterally. The lateral edges, defined between the posterior discal edge and the posterolateral apices of the slender arms, run evenly concave. The whole sternum is a well sclerotized structure reinforced along its entire anterior edge by the conspicuous antecostal ridge, which projects dorsally on the ventral surface and defines the very brief acrosternite, noticeable mesally. The anterolateral apices of the sternal arms bear the sternal apodemes (Fig. 1). The lines of insertion of the conjunctiva that connects with the eighth metasomal sternum are located on the ventral surface of the disc.

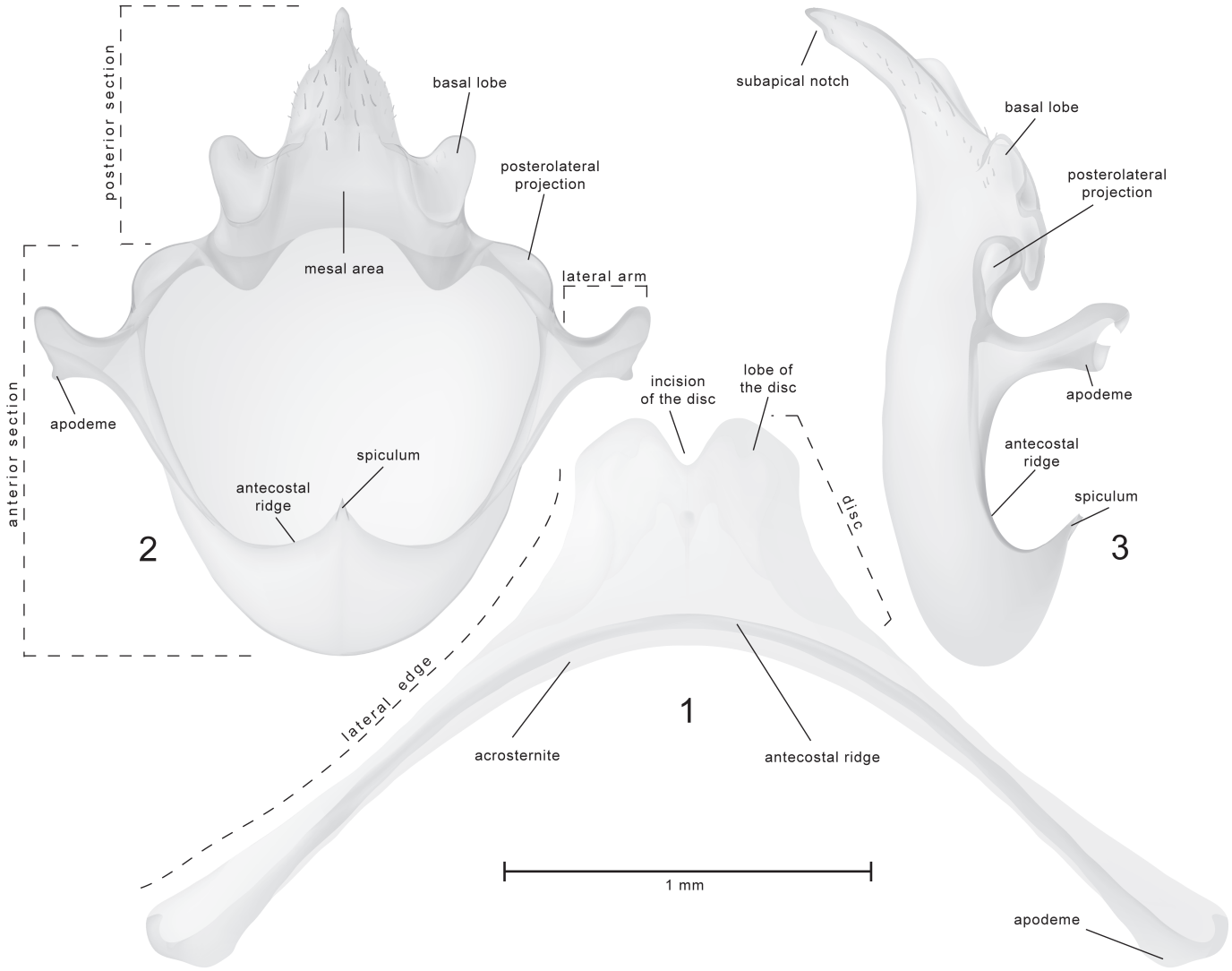
This kind of seventh metasomal sternum, with a bulky trapezoidal disc and devoid of setae (see below), is typical of the subgenera *Glossura*, *Glossuropoda*, and some species of *Glossurella*.

There is significant taxonomic and systematic value in the features of the seventh metasomal sternum. The basic construction of the sternum in the species of *Euglossa* as well as in the rest of euglossine genera follows the scheme described for *E. imperialis*; however there are variations that give great value to the study of this sclerite. The most significantly variable features of this sternum involve the disc, particularly its posterior edge, which in the majority of the species bears an incision (as described above), with depth and shape in most cases being species specific, although exceptions can be found in groups like *E. decorata* and allied species, which show a range of intraspecific variation (Hinojosa-Díaz, in prep.). The posterior edge is entire in some species, especially of *Eufriesea* (e.g., Kimsey, 1982), as well as in *Exaerete*, in which it sometimes has a mesal acute projection instead of an incision (Kimsey, 1979; Anjos-Silva *et al.*, 2007). The discal lobes resulting when the edge is notched are also variable in shape and orientation. A feature of most euglossine species, absent in *E. imperialis*, is the presence of setae on the posterior edge of the seventh metasomal sternum, sometimes restricted to the disc (notched or not) but often sparsely extended to areas on the lateral edges proximal to the disc. The lateral edges of the sternum can be slightly concave, as in *E. imperialis*, or slightly convex, this affected by the length and shape of the disc. Some species of *Euglossa* (e.g., Hinojosa-Díaz and Engel, 2007) as well as of *Eufriesea* (e.g., Kimsey, 1982) and *Eulaema* (e.g., Oliveira, 2006) have either protuberances or notches along this lateral edge. The seventh metasomal sternum of *Bombus* lacks long arms so the lateral edges are defined mainly by the lateral edges of the disc. Otherwise the posterior edge presents features similar to those of Euglossini (Ito, 1985). In Meliponini the sternum is reduced to a small plate (Michener, 2007). Centridini and Anthophorini have seventh metasomal sterna in which the arms are clearly differentiated but never as long as in Euglossini and with an entire posterior edge (e.g., Brooks, 1988; Ayala, 1998).

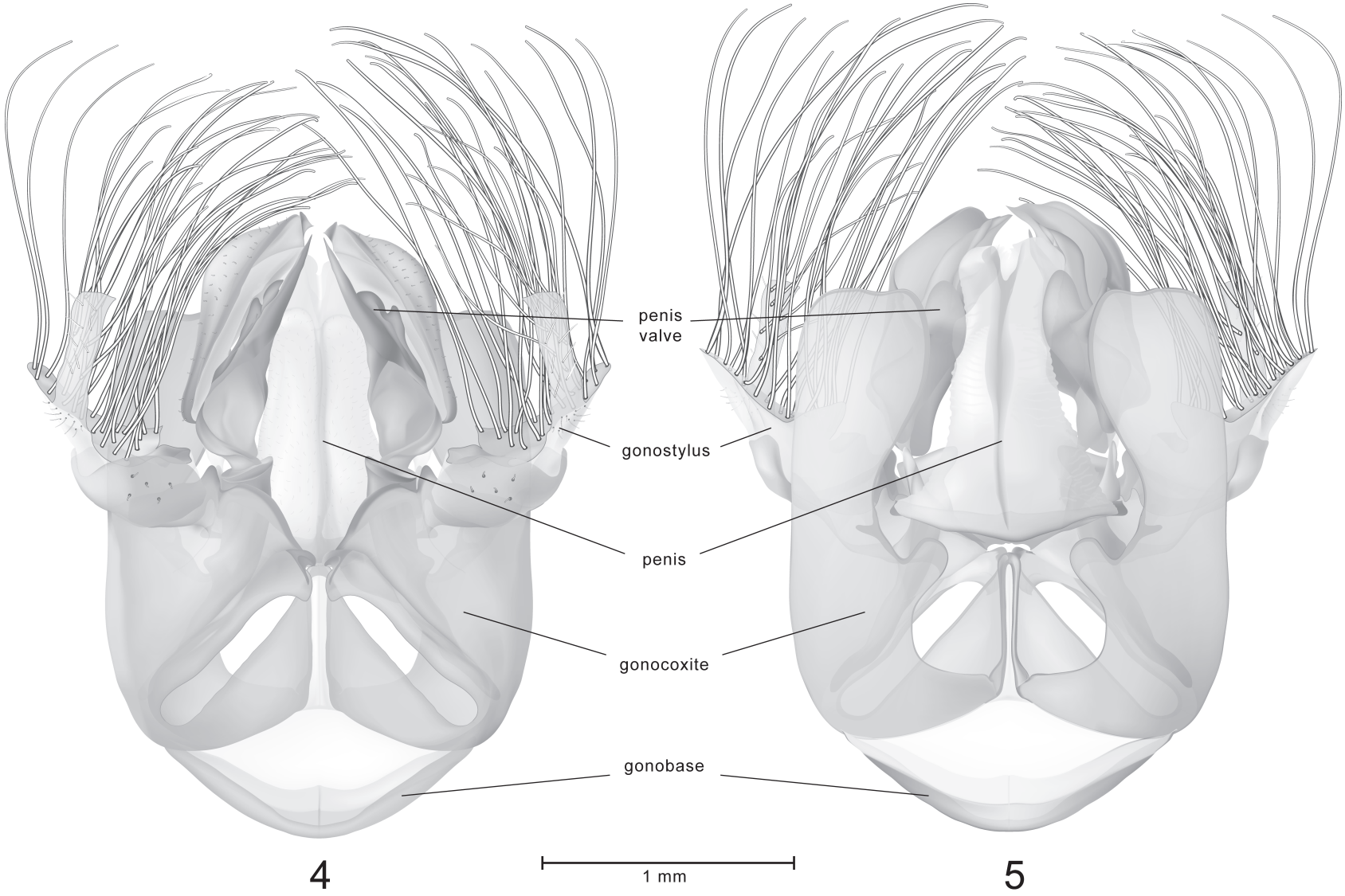
Eighth metasomal sternum.—The eighth metasomal sternum (usually referred to as S8), rests between the seventh metasomal sternum and the genital capsule, all invaginated in the metasomal apex, as mentioned before. As is the norm for bees and other Hymenoptera (Michener, 1944a, 1956), the eighth metasomal sternum is substantially different from the rest of the metasomal sterna. In *E. imperialis* in particular, and Euglossini in general, these differences are marked. Instead of being a depressed sclerotic plate as are the rest of the sterna, this sternum is strongly three-dimensional. In a simplified view it is formed by two main sections plus the short lateral arms (Fig. 2). The anterior section, with a depressed globular shape, provides most of the surface and volume of the sternum; in dorsal and ventral views, it looks roughly ovoid, wider posteriorly, with two convex posterolateral sclerotic thickenings projected outwards flanking the posterior section of the sternum. The dorsal surface of the posterior section is completely open, bearing the posteriorly-projected spiculum. The posterior section of the sternum projects from the ovoid anterior section and is hollow and roughly triangular with two lateral basal lobes (Fig. 2). In lateral view the posterior section is projected ventrally, forming an angle of about 140° degrees with the longitudinal axis of the anterior section (Fig. 3). The arms come from the mesoposterior portions of the anterior section of the sternum and project laterodorsally, bearing the small apodemes at their anterior corners (Fig. 2).

The extreme morphology of the eighth metasomal sternum can be explained by looking at it in terms of a modified flat sternum. The globular posterior section is the product of the inflection dorsally of the anterior edge that curves posteriorly, and the basalmost section of the disc projects anteriorly forming the rounded anterior

apex of the ovoid shape. The antecostal ridge, as a result, is projected ventrally towards the inner cavity of the sternum, while there is no clear evidence of the acrosternite. The mesally-located spiculum is also, as a consequence of the inflection of the anterior edge, directed posteriorly on the now anterodorsal edge; the spiculum is unque to the eighth metasomal sternum and in most bees projects anteriorly rather than posteriorly (Michener, 2007); the posteriorly projected spiculum was called "notospiculum" by Hinojosa-Díaz and Engel (2007). The relatively complex structure of the posterior section of the eighth metasomal sternum likewise involves inflection of edges and projection of the discal surface; however it is not easily explained, since there are no clear clues. Nonetheless, the structure of the posterior section deserves extra consideration. Its dorsally basal (anterior) edge is strongly sclerotic with a series of folds (continuing from the posterolateral sclerotic projections of the anterior section of the sternum), and two projections directed anteriorly. The dorsal surface is elevated posterior to the two projections. Each elevated sector ends in a carina that flanks the basal and lateral sides of the basal lobes, which in turn are a product of the invagination of the lateral edges of the triangular shape. The two elevated sectors define a smooth, depressed mesal area (Fig. 2). The remainder of the anterior section, beyond the basal lobes, is basically the one deviating from the longitudinal axis of the sternum, as seen in lateral view (Fig. 3). This area is covered with scattered, short, simple setae on its dorsal and lateral surfaces and bears, dorsally, a mesal ridge that rises evenly, end-



Figs. 1-3. *Euglossa imperialis*, male hidden metasomal sterna. 1. Seventh metasomal sternum, ventral view. 2. Eighth metasomal sternum, dorsal view. 3. Eighth metasomal sternum, lateral view.



Figs. 4-5. *Euglossa imperialis*, male genital capsule. 4. Ventral view. 5. Dorsal view. The setae on the gonostylus are depicted at a lower density than they appear on all observed specimens.

ing midway towards the posterior apex. This ridge seems to be a variable feature within the species, since in some specimens it is just briefly insinuated. The apex of the sternum narrows abruptly in lateral view at around the last third of its length, and bears a ventral subapical notch (Fig. 3).

The systematic and taxonomic value of the traits seen in the eighth metasomal sternum are relevant within *Euglossa* and Euglossini. The shape of the anterior globular section varies little among *Euglossa* species, for the most part being as described above. In the other euglossines, *Eufriesea* and *Exaerete* have an eighth metasomal sternum similar to that of *Euglossa*, longer in *Eulaema* and *Aglae*. The spiculum is extremely reduced in Aglae. The shape and length of the lateral arms present some variation among *Euglossa* species, as well as in the other genera. The posterolateral projections of the anterior section seem to be present in all euglossine species, except in *Aglae*; their shape, evenly roundly convex in *Euglossa*, is otherwise acutely projected in *Eufriesea*, *Eulaema*, and *Exaerete*. Of considerable value is the variation observed in the posterior section of the sternum. The basal lobes and associated invaginations of the lateral integument of the triangular apex, seem to be important in defining infrageneric assemblages, as they are presently understood in *Euglossa*. The species generally classified under *Euglossa sensu stricto* show just slightly projected basal lobes, having an almost perfectly triangular posterior section of the eighth metasomal sternum. Very well developed lobes as seen in *E. imperialis*, are found in all species of *Euglossella*, *Glossura*, *Glossuropoda*, and most of *Glossurella*. Of the remainder of euglossine genera, *Eufriesea* and *Eulaema* are the only ones with evident basal lobes in the posterior section, but theirs are acute projections (e.g., Kimsey, 1982; Oliveira, 2006), while in *Euglossa*, when present, these are rounded convexities, for the most part. The very apex of the posterior section is also variable among groups in *Euglossa*. It is narrower, in dorsal, ventral, or lateral views in almost all species with well-developed basal lobes. The shape of the posterior section in *Eufriesea* is also triangular and narrow, although with different conformation than in *Euglossa* (e.g., Kimsey, 1982). The same can be said for *Eulaema*, but here the apex after the basal lobes may take oval shapes (e.g., Oliveira, 2006). In *Exaerete* the apex of the posterior section is broadly rounded or truncate (Kimsey, 1979), while in *Aglae* it appears like an unmodified rectangular projection with rounded sides. The subapical ventral notch, present in most species of *Euglossa*, is absent in *E. villosa*. The notch is also present in species of *Eufriesea* (although larger [Kimsey, 1982]) and *Eulaema*, and absent in *Exaerete* and *Aglae*. The setae on the posterior section are also good characters to distinguish species and perhaps species groupings in *Euglossa*. Most species

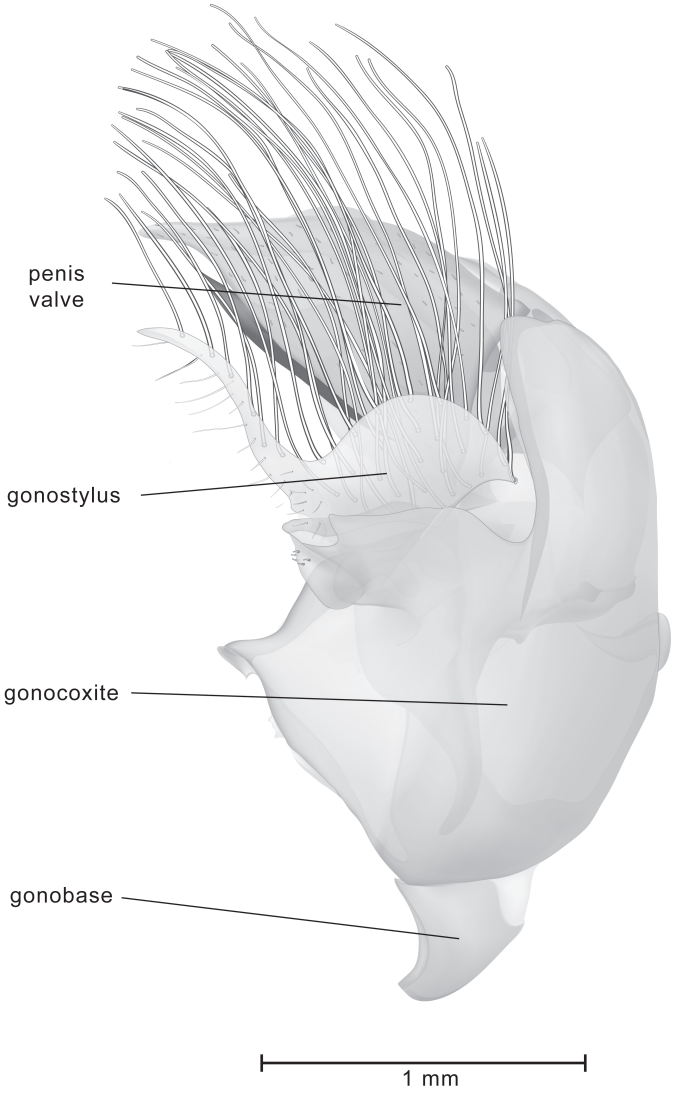


Fig. 6. *Euglossa imperialis*, male genital capsule, lateral view. The setae on the gonostylus are depicted at a lower density than they appear on all observed specimens.

have pilosity as described for *E. imperialis*, but relatively long plumose setae on the ventral surface are characteristic of most species of *Euglossella* (e.g., Hinojosa-Díaz and Engel, 2007). In *Bombus*, the eighth metasomal sternum is rather flattened; the spiculum is where most of the variation occurs, and the posterior section is morphologically simpler than in Euglossini (Ito, 1985). In Meliponini the eighth metasomal sternum is reduced or absent (Michener, 2007). In Centridini this sternum is flat, but seemingly not as flat as in *Bombus*; both groups of bees have the spiculum directed anteriorwards, the anterior edge not curved posteriorly (or just slightly), and a posterior section of varied shape (e.g., Ayala, 1998). Some subgenera of *Anthophora* have a posteriorly inflected anterior edge

and a spiculum directed dorsally or posteriorly (Brooks, 1988), but the sternal disc is never anteriorly evaginated as in the globular-shaped sternum of Euglossini.

Genitalia.—The male genitalia, or genital capsule, of *E. imperialis* is a heavily sclerotic structure consisting of individual units that articulate or link to form the copulating apparatus. It is hidden at the posterior apex of the metasoma, overlaying the hidden sterna. The distinct recognizable parts composing it are: gonobase, gonocoxites, gonostyli, and aedeagus (Figs. 4-6).

Gonobase.—The most anterior component of the male genitalia in *E. imperialis*, the gonobase, is a sclerotic plate about three times as wide as long, inflected in such a way that its convex surface arches forming an extended bowl-shaped structure, running mainly dorsolaterally, and attached to the gonocoxites via its postelolateral edges (Figs. 7-9). The ventral edge is bent posteriorly and firmly sclerotic. A soft mesal line divides the gonobase into lateral symmetrical halves, while defining a small dorsomesal projection. Dorsally the convex blade weakens as it runs posteriorly to meet the gonocoxites, making it hard to find the limit between the sclerite and the continuing membrane that closes the dorsal section between gonobase and gonocoxites. In lateral view the anteriormost section of the ventral edge projects ventrally (Fig. 8).

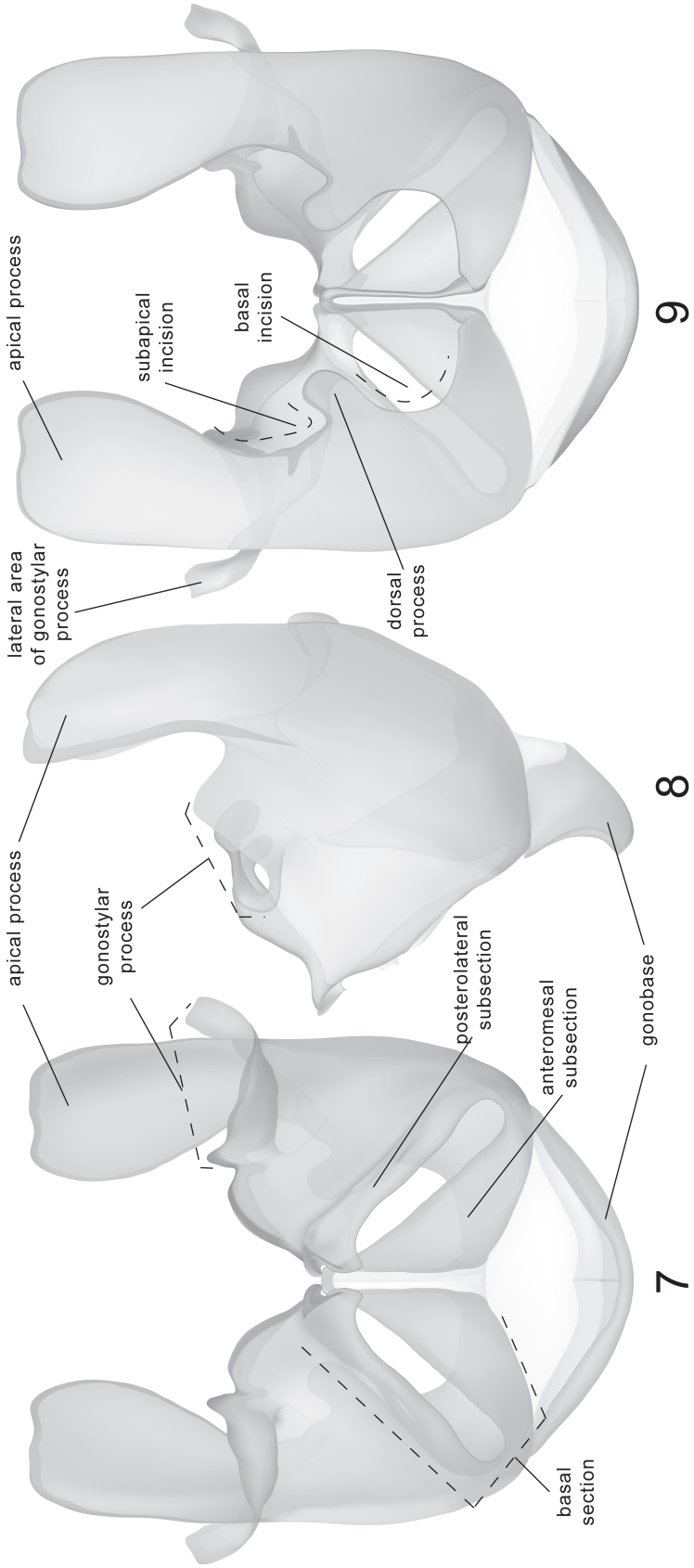
The variation observed in the gonobase of all euglossine species involves basically its length and width. An important species-specific character seems to be the way the ventral edge projects on its anterior section, or if it does not project at all (e.g., Hinojosa-Díaz and Engel, 2007).

In *Bombus* the gonobase is a complete sclerotized ring enclosing the genital foramen, although the ventral section is considerably narrower than the dorsum, sometimes appearing as fused to the gonocoxites (Ito, 1985). In Meliponini this structure is reduced as a whole, present as a very narrow dorsal belt (Camargo *et al*., 1967; Michener, 2007). The ventral part of the ring is obviously absent in Euglossini (i.e., membranous), and is generally very narrow in Centridini and Anthophorini, looking almost absent in some species of *Centris* (e.g., Ayala, 1998).

Gonocoxite.—The pair of gonocoxites constitutes the bulkiest part of the genitalia. Viewing the insect male genitalia as homologous to walking appendages, the gonocoxites plus the gonobase would correspond to the basal segments of the outer section of the embryonic claspers (Michener, 1944a, 1956); this is important in terms of the name of the structure. In *E. imperialis* each gonocoxite is a strongly-sclerotic unit with a well defined basal (anterior) section, and the main body of the gonocoxite as a laterally convex structure open towards the inner area where the aedeagus is located (Figs. 7-8). The basal section corresponds to the anterior surface of the gonocoxite, forming a posterolateral wall to each side of the genital foramen. In a comparative study of the male genitalia of Andrenidae, a likely homologous structure to the basal section is referred to as the gonocoxal apodeme (Rozen, 1951). The basal section is divided by a deep diagonal incision through which musculature and the ejaculatory ducts pass. The triangular, anteromesal subsection defined by the incision, connects on its inner mesal edge (reinforced by a dorsal inflection), with the corresponding subsection of the opposite gonocoxite (Fig. 7). This longitudinal membranous connection articulates both gonocoxites in a hinge fashion, giving them a forceps like movement. The posterolateral subsection is narrow, broadened on its posteromesal extreme with an acute projection directed anteriorly, and with a strong carina on its apex. The apical projection of the carina forms the second point of articulation with the opposite gonocoxite. Both subsections, are differentially oriented forming an acute separation angle, at the anterior extreme of the incision, that increases or decreases as the gonocoxites move acting as forceps.

The main body of the gonocoxite is strongly concave continuing from the basal section, and with distinctive processes on its dorsal and ventral surfaces. The dorsal surface of the body of the gonocoxite rises convexly from the anterodorsal edge of the basal section. It is dominated by two processes, a dorsal process projected posteromesally, and a larger apical (posterior) process. The dorsal process is a thumblike projection of the dorsomesal edge, slightly longer than wide and evenly rounded apically; the apex of the dorsal process is reinforced by an infold (Fig. 9). The dorsal process separates two major incisions, one basal and another subapical. The basal incision is evenly concave, while the subapical incision forms an acute angle with the dorsal process. The subapical incision precedes the large apical process, which is a projection of the whole dorsal surface of the gonocoxite. The apical process is a hollow flattened structure with sharp, carinate edges, and a short perpendicular thickening at the concave edge of the subapical incision (Figs. 7-9). The inner edge of the apical process, immediately after the subapical incision, is convex, making the process wider near its apex. The posterior edge is truncate with a minor emargination proximal to the posteromesal corner. The straight outer edge of the apical process meets basally with the gonostylar process of the ventral surface of the gonocoxite (see below).

The ventral surface of the gonocoxite continues from the posterior edge of the basal section after a sharp bend. It is rather flat ventrally (Fig. 7), becoming convex laterally (Fig. 8) to converge with the dorsal surface. The inner edge is posteromesally convex and is hardened by infolds and thickenings; two strong prong-like projections, directed towards the lumen of the genital capsule, are located at the posteromesal angle. The ventral surface bears



Figs. 7-9. *Euglossa imperialis*, male gonocoxites. 7. Ventral view. 8. Lateral view. 9. Dorsal view.

apically its main feature, the gonostylar process, which is a ventrolateral projection with a basket-like shape where the gonostylus rests (Figs. 4-6). The gonostylar process extends laterally beyond the outer edge of the gonocoxite and is reinforced by infolds (Figs. 7-9). The whole lateral section of this process is fused to the thin sclerotic blade of the ventral section of the gonostylus (Figs. 4-6); however the border between both structures can be recognized on the basis of change of thickness of the sclerotic blade.

The inner concavity created by the gonocoxites is occupied by soft tissue and by the apodemes of the penis valves (Figs. 4-6). The open areas between the inner edges of the dorsal and ventral surfaces are protected by membranes.

The morphology of the gonocoxite is a good source of characters of definite taxonomic and systematic value. Perhaps the most noticeable feature of the gonocoxite of *E. imperialis* is the large apical process. The variation of this structure within *Euglossa* involves the alignment of its posterior edge. As seen in *E. imperialis* this edge is perpendicular to the sagittal plane of the genital capsule (Fig. 5), a condition found in all species of *Glossura* and seemingly all *Euglossa sensu stricto*, as well as in some *Glossurella* (e.g., Parra-H *et al.*, 2006; Rasmussen and Skov, 2006). In the subgenus *Euglossella* (and some *Glossurella*) this edge is oblique, having the posterolateral corner displaced anteriorly, making the apical process look acute in dorsal view (e.g., Hinojosa-Díaz and Engel, 2007), while in *Glossuropoda* the opposite oblique situation is observed. The carina of the posterior edge is in some species slightly projected especially the corners, making it shallowly concave. In the other euglossine genera the edge is rather oblique the way it is in *Glossuropoda* (the opposite to that of *Euglossella*), although in some of them it is hard to evaluate this situation, especially in *Eufriesea* in which the edge is deeply concave (e.g., Kimsey, 1982), being just slightly concave in *Eulaema* and *Aglae*, and slightly convex in *Exaerete* (e.g., Anjos-Silva and Rebêlo, 2006). The apical process is larger in *Euglossa* than in the rest of the Euglossini. This process seems to be present in *Bombus* as a posterior enlargement; however, it is not a free apical projection since it bears on its apex the structure homologized with a gonostylus by Michener (2007), and called the squama by Ito (1985). In Meliponini the apical process seems to be present in some groups, but reduced and with varied shape. The apical process is absent in Centridini and Anthophorini. The dorsal process is also subject to variation, in *Euglossa* varying in shape and orientation, which in turn alters the shape of the basal and subapical incisions, particularly the latter. The variation in shape of the dorsal process and adjacent incisions seems to be species specific, varying among species of the same subgenus. This process is present in the other euglossine genera except *Aglae*. The basal incision is noticeably concave throughout all *Euglossa* species, while in *Eufriesea*, *Eulaema*, and *Exaerete* it can hardly be considered an incision since the inner edges of the dorsal surface of both gonocoxites run parallel to each other, basal to the dorsal process. *Bombus* has a dorsal process located in a more basal position than in Euglossini; therefore the basal incision is shorter and the subapical incision enlarged (e.g., Ito, 1985). No dorsal process is seen in Meliponini. Several groups of Centridini have a dorsal process, with various shapes as well as a basal incision also varied. In Anthophorini there is no obvious dorsal process although the convexity of the basal inner edge of the dorsum of the gonocoxite could be mistaken for it. In *Euglossa* the gonostylar process also shows substantial variation, which is correlated with the variation of the gonostylus (see below).

In general the larger gonostylar processes, with well differentiated basket surfaces, are found in *Glossura*, *Glossuropoda*, and some *Glossurella*, while in the rest of the species the process is rather small. Only in the aforementioned groups (not in all species of *Glossurella*) is the gonostylar process fused to the gonostylar blade. In the rest of the species of *Euglossa* the lateral edge of the gonostylar process barely exceeds the lateral margin of the gonocoxite, and besides not being fused to the gonostylar sclerotic lamina, it can have acute, truncate, rounded or prong-like shapes. The inner delimitation of the gonostylar process also varies in its separation from the posteromesal prongs of the inner ventral edge, being almost contiguous in most *Glossura*, and some *Glossurella*, and of varied nature in other groups. The gonostylar process of the other euglossine genera is, despite the different opinion of Kimsey (1987), not as developed as the one described here, being more similar to the one seen in species of *Euglossa sensu stricto*; however, in both *Eufriesea* and *Eulaema*, the lateral projection of the process is rather slender and setose on its apex. In the other corbiculate and non-corbiculate apine bees, used here for comparison, there is no strong modification of the ventral surface of the gonocoxite to support the gonostylus.

Gonostylus.—The gonostylus of *E. imperialis* is a very noticeable structure arising from the gonostylar process of the gonocoxite. It is mainly membranous, setose, and composed of two main parts, a ventral section and a lateral section (Figs. 10-12). The ventral section has been treated differently, as can be seen in Table 1, sometimes as part of the gonostylus (Michener, 1944a), as the sole gonostylus (in *Bombus* [Ito, 1985]), as a different structure called the volsella (Kimsey, 1987; Michener, 2007), or ignored as a gonostylar component (Ospina-Torres *et al.*, 2006). Here this section is discussed as part of the gonostylus since it is structurally connected to the lateral section. The term volsella as used by Kimsey (1987) and Michener (2007) in Euglossini (also in Bombini by the second author) is par-

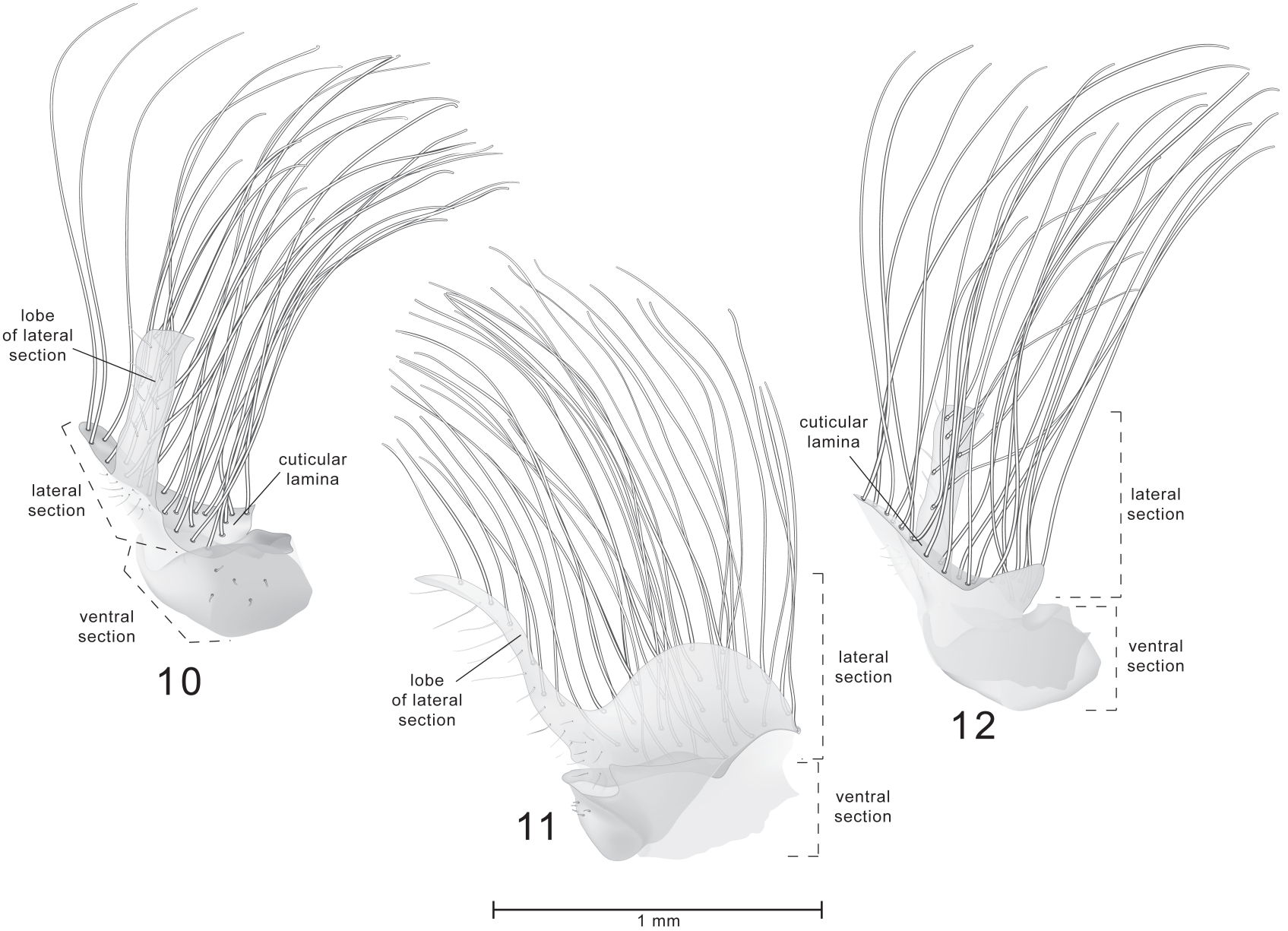
ticularly misleading. This gonostylar section is not homologous to the pinching structures found in the genital capsule of other Hymenoptera, including other groups of bees, and as such the term volsella should be avoided in this context. The bulky membranous ventral section of the gonostylus is continuous on its posterolateral area with the lateral section of the gonostylus (Fig. 6); it is roughly rod-shaped, running dorso-ventrally, with its ventral half resting entirely on the basket of the gonostylar process of the gonocoxite. The oval, flat ventral surface of the ventral section, exceeds the gonocoxite basket edge. The dorsum of the ventral section is embedded in the lumen of the genital capsule (Fig. 6). The overhanging ventral surface, as well as the posterior and lateral surfaces, are covered with a continuous cuticular layer (Fig. 10). This lamina is connected laterally to the lateral projection of the gonostylar process of the gonocoxite, and is continuous with the inner surface of the lateral section of the gonostylus. As mentioned before, gonostylus and gonocoxite are fused on the lateral projection of the gonostylar process, but the limit of both structures can be traced by the changes in thickness of the sclerotized continuous cuticle. The ventral overhanging surface is flat and centrally covered with sparse, minute, simple setae.

The conspicuous lateral section of the gonostylus, also membranous, rests posterolaterally to the ventral section, as a free projection. It is somewhat compressed, diagonally oriented, and scoop-shaped if seen from the middle axis of the genital capsule (Figs. 10, 12). In lateral view, the posterior edge of the gonostylar lateral section is convex on its dorsal main sector (Fig. 11), while ventrally it bears a slender membranous lobe that appears rectangular in ventral or dorsal views (Figs. 10, 12). The whole inner surface, including the lobe, is covered by the cuticular lamina that joins it with the posterior surface of the ventral section of the gonostylus, from which it can be differentiated by a shallow channel and by the presence of dense, long, simple setae covering the entire inner surface, including the lobe. The outer (ventral) surface of the lobe is covered by sparse, short, simple setae (Figs. 10-12).

The gonostylus is perhaps the most diversified structure of the genital capsule of *Euglossa*, and is as such of substantial taxonomic and systematic value in terms of infrageneric assemblages. The ventral section is generally overhanging, but this is definitely much more noticeable in species of *Glossura*, *Glossuropoda*, and some *Glossurella*. The rest of the species have a ventral section not as large, just surpassing the basket edge, and the ventral surface is convexly projected, while in the aforementioned groups it is rather flat, truncate (as described for *E. imperialis*). A feature that covaries with the overhanging ventral section is the presence of the continuous cuticular lamina connecting the ventral section with the lateral section, as well as with the gonocoxite on its gonostylar process. In those species in which the ventral section is neither bulky, nor strongly overhanging, the gonostylar process of the gonocoxite, the lamina of the posterior surface of the ventral section, and the inner surface of the lateral section, is only connected on its dorsalmost extreme, while there is no continuity between the ventral lamina and the lateral part of the gonostylar process of the gonocoxite, which according to Kimsey (1987), is considered the derived condition in Euglossini. The minute setae on the ventral section are usually on the ventral overhanging surface, but in some species they are also on the inner or posterior surfaces.

The variation of the lateral section of the gonostylus deserves special attention. Ospina-Torres *et al.* (2006), in their brief comparative study of this structure in *Euglossa*, proposed five different arrangements, mainly based on its division into two lobes. Their "ventral lobe" is the slender lobe here described for *E. imperialis*, and their "dorsal lobe" would be equivalent to the dorsal sector of the lateral edge, which is noticeably convex. Although in a lateral view this latter feature can certainly be considered a lobe, it is more accurate to look at the structure on its whole shape, not just laterally. In doing so, it seems more reliable to consider this just as a strongly convex edge of the setose dorsal sclerotic blade of the gonostylus. Ospina-Torres *et al.* (2006), examined the gonostylar lateral sections by mounting them on flat slides, not considering the whole tridimensional arrangement of it as it is situated on the gonocoxite. This arrangement is important, having two alternatives: the dorso-posterior blade (i.e., the cuticular blade bearing the long setae) oriented diagonally (as in *E. imperialis*), in all species of *Euglossa sensu stricto* (e.g., Bembé, 2007), *Glossura* and *Glossuropoda*, and some *Glossurella*, or the dorso-posterior blade almost totally compressed and oriented straight posteriorly, as in most *Glossurella*, and all *Euglossella* species. Nonetheless, the nature of the posterior edge (rather lateral in the diagonally-oriented blades) is also valuable in a taxonomic and systematic context. Clearly convex in several groups (as in *E. imperialis*), it appears flat, or even concave in some species; in some cases the basal sector is either enlarged with a minute ventral lobe, or reduced with a dominant ventral lobe. The location, density, and nature of the setae on the lateral section of the gonostylus also vary considerably. The longer setae are always on the dorsal blade, sometimes being plumose as in *Euglossella* species (Hinojosa-Díaz and Engel, 2007), while the ventral, or lateral surfaces of the ventral lobe bear sparse, simple, minute setae. Some species have the gonostylus almost devoid of setae, noticeably *E. nigrosignata* and *E. oleolucens*.

It is important to mention that beyond the usefulness of the gonostylar morphology to define infrageneric assemblages in *Euglossa*, there are differential cases of their



Figs. 10-12. *Euglossa imperialis*, right male gonostylus. 10. Ventral view. 11. Lateral view. 12. Dorsal view. The setae on the gonostylus are depicted at a lower density than they appear on all observed specimens.

application to determine species boundaries. Most of the species in the genus have a particular morphology with little variation as is the case of *E. imperialis*, but there are cases like *E. decorata* and allied species in which there seems to be a great deal of intraspecific variation in gonostylar morphology (Hinojosa-Díaz, in prep.) although all of it within the overall morphology that characterizes *Euglossella*.

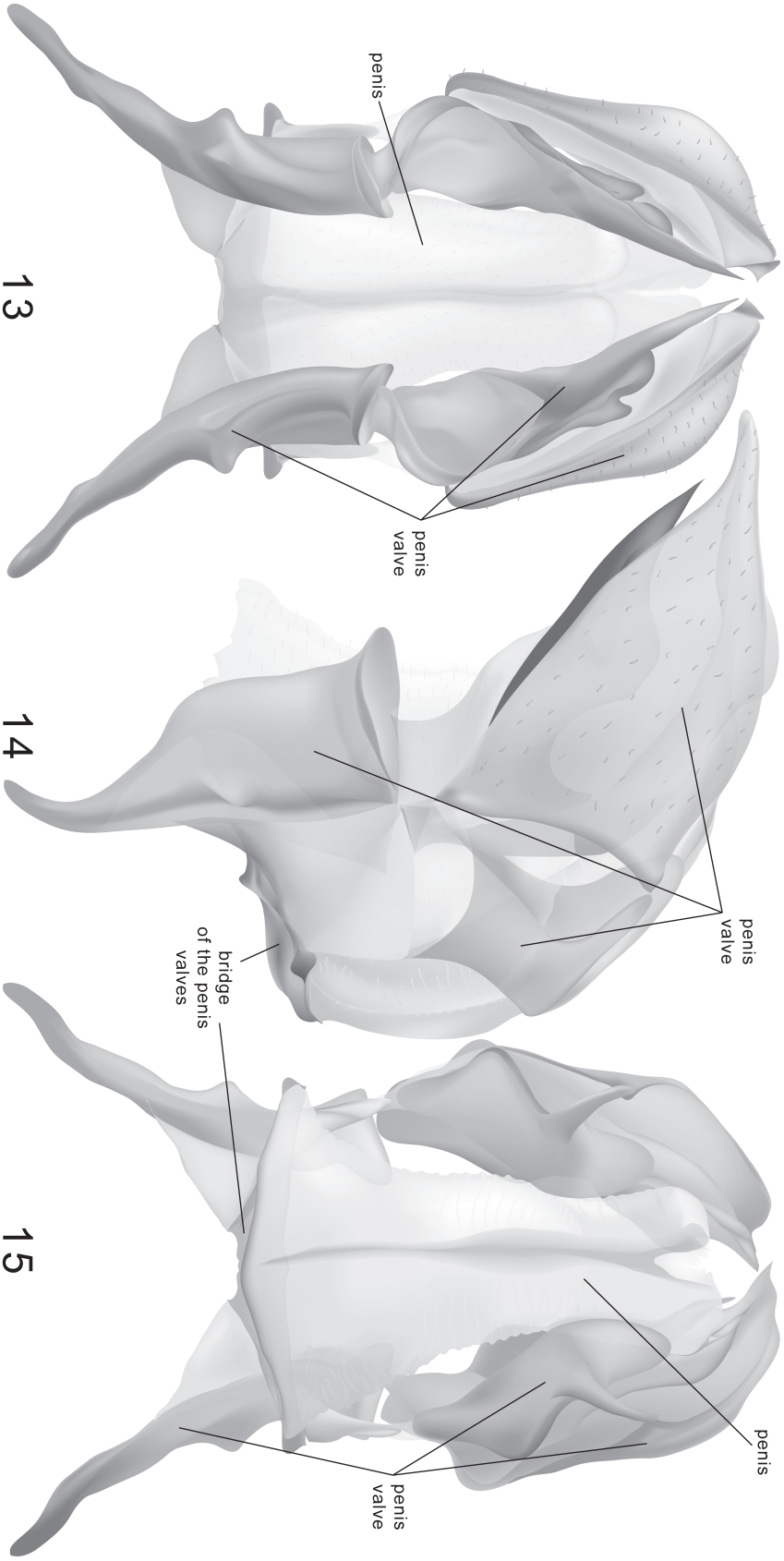
The gonostylar variation in other euglossines occurs mainly in the lateral section (i.e., the one treated as gonostylus). In *Eufriesea* it is laterally compressed, not diagonal, appearing more sclerotized than in *Euglossa*, but most importantly, strongly bilobate. The large dorsal lobe is probably homologous to the dorsal sector of the lateral section of the gonostylus of *Euglossa* judging by the disposition of the setae. In *Eulaema* and *Aglae* the also sclerotic laterally-compresed lateral section of the gonostylus consists of a simple lobe, with just a small dorsal bump seemingly homologous to the dorsal sector. In *Exaerete* the membranous lateral section of the gonostylus has a ventral rod-shaped lobe, and a flat and small dorsal sector (Kimsey, 1979). In *Bombus* the ventral section (treated in other studies as volsella [Kimsey, 1987; Michener, 1990, 2007], or as the exclusive gonostylus [Ito, 1985]) is considerably sclerotized and larger than in Euglossini, lying apically on the unmodified ventral area of the gonocoxite, and with apical modifications (Ito, 1985). The lateral section (treated in other studies as the squama [Ito, 1985]), also sclerotic, is rather subapical on the dorsal surface of the gonocoxite. In Meliponini the gonostylus is represented by a single slender lobe coming from the base of the gonocoxite. In Centridini and Anthophorini, all the features of the gonostylus observed in Euglossini are found, with a range of variation entirely their own.

Aedeagus.—This is the structure between the gonocoxites, composed of the strongly sclerotic penis valves articulated at each side of the penis (Figs. 13-15). The aedeagus is joined to the genital capsule by the insertion of the apodemal projection of each penis valve into the lumen of the gonocoxites (Figs. 4-6).

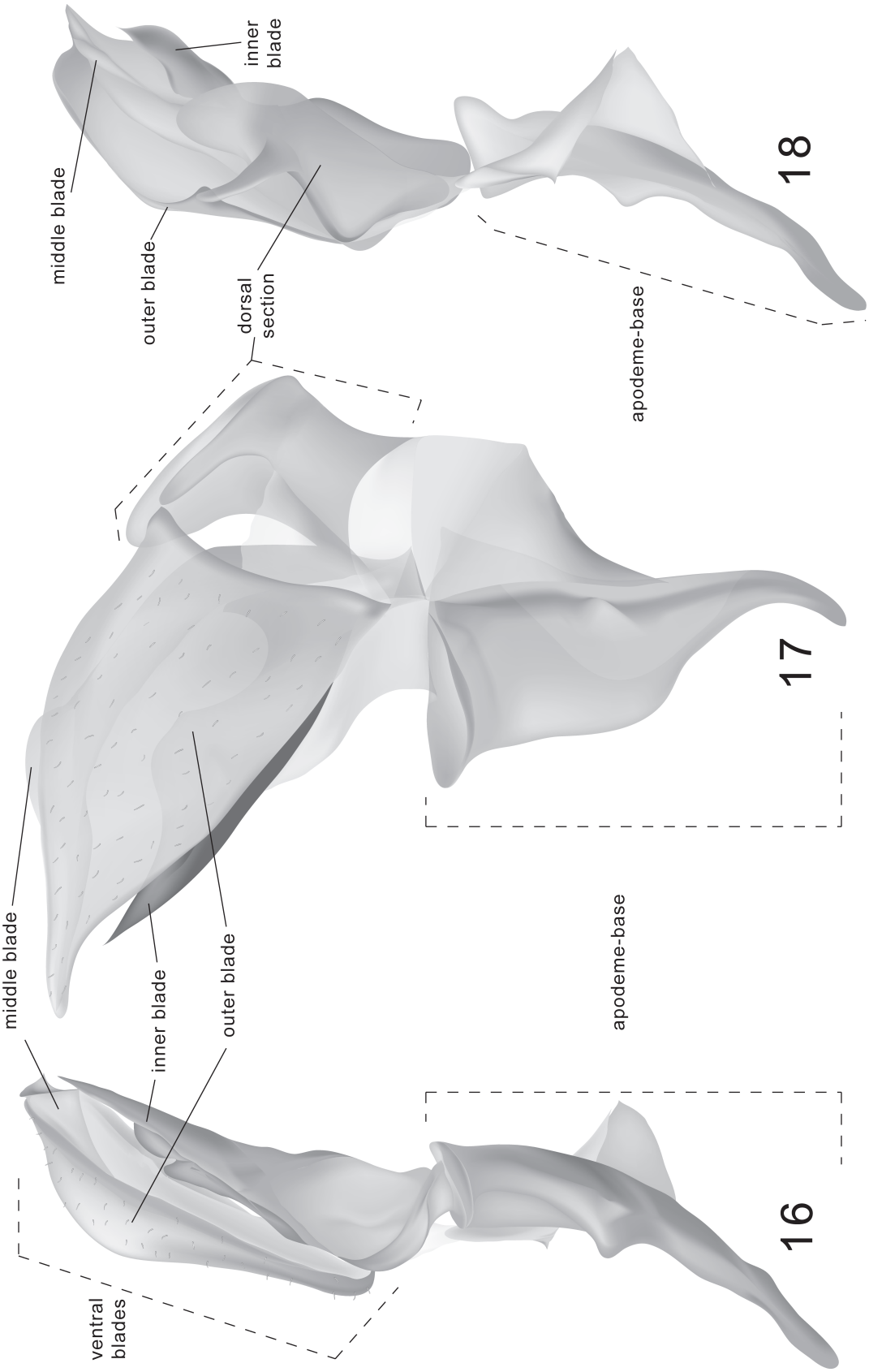
Penis valve.—Following the idea that the insect male genitalia is homologous to walking appendages, the penis valves would correspond to the inner section of the embryonic claspers (Michener, 1944a, 1956). Each penis valve is a sclerotic structure with membranous areas connecting three distinguishable sections: apodeme-base, dorsal section, and ventral blades (Figs. 16-18). The apodeme-base is the most anterior section. It is a somewhat compressed, cone-like structure, that takes about half of the total length of the valve, and is the one by which each valve is united to the rest of the genital capsule. The attaching acute apodeme is embedded in the inner matrix of the capsule, at the base of the gonocoxite, is curved ventrolaterally towards the lateral wall of the gonocoxite. Outside the lumen of the gonocoxite this section widens dorsoventrally and an acute prong is projected laterally (Fig. 16). The dorsal side of the apodeme-base bears a lamella extending in two directions; the anterior part is directed mesally while the posterior part extends posteriorly following the orientation of the whole penis valve. The fold that delimits the two lamellar sections strengthens the anterodorsal edge of the apodeme-base and projects dorsally in an acute angle. The anterior part of this lamella articulates with the bridge of the penis valves and the posterior part does the same with the dorsal section of the penis valve (Figs. 14-15). The ventral side of the apodeme-base takes up most of the posterior widening of the conic shape. The posterior surface takes a scoop-like shape with a carinate edge, and leans slightly towards the gonocoxite. This posterior widened area of the apodeme-base lies close to the pair of strong, prong-like projections of the ventral surface of the gonocoxite (Fig. 4). The scoop-like posterior surface is articulated to the ventral blades of the penis valve by a sinuate, slightly-sclerotic membranous fold.

The dorsal section of the penis valve consists of a sclerotic unit with a compressed trapezoidal shape, running anteroposteriorly, the posterior part broadened and divided laterally in two prong-like projections, one on each side, forming a posterior concave surface (Figs. 17-18). The inner prong is larger. The whole dorsal section, as mentioned above, articulates anteriorly with the apodeme-base and ventrally, via weakly sclerotic and membranous segments, with the ventral blades.

The ventral blades section of the penis valve comprises three compressed blade-like structures appressed one against another and oriented dorsoventrally. The outer blade has a sublanceolate shape, with all edges folding towards the meson (Fig. 17). It articulates with the dorsal section of the penis valve via a membrane attached to its strong, rather truncate dorsal edge, and with the scoop-like posterior surface of the apodeme-base via a sinuate slightly sclerotic membranous fold. The entire outer surface of the outer blade is covered with sparse, minute setae. The middle blade is strongly sclerotic on its dorsal and posterior margins, being attached to the mixture of sclerotic and membranous junctures that come from the dorsoposterior area of the apodeme-base. The rest of the middle blade is rather membranous and united to the outer blade all along its anterior edge, both blades together forming a sort of compressed sheath. The inner blade is the most sclerotized and runs along the anterior edge of the other two blades. It is joined to the rest of the penis valve on the same sclerotic-membranous juncture coming from the dorsoposterior area of the apodeme-base. This inner blade has a knife-like shape, with a very acute ventral apex and a series of thickenings and convolutions on its posterior edge (Figs. 16-18). Each penis valve serves as



Figs. 13-15. *Euglossa imperialis*, aedeagus. 13. Ventral view. 14. Lateral view. 15. Dorsal view.



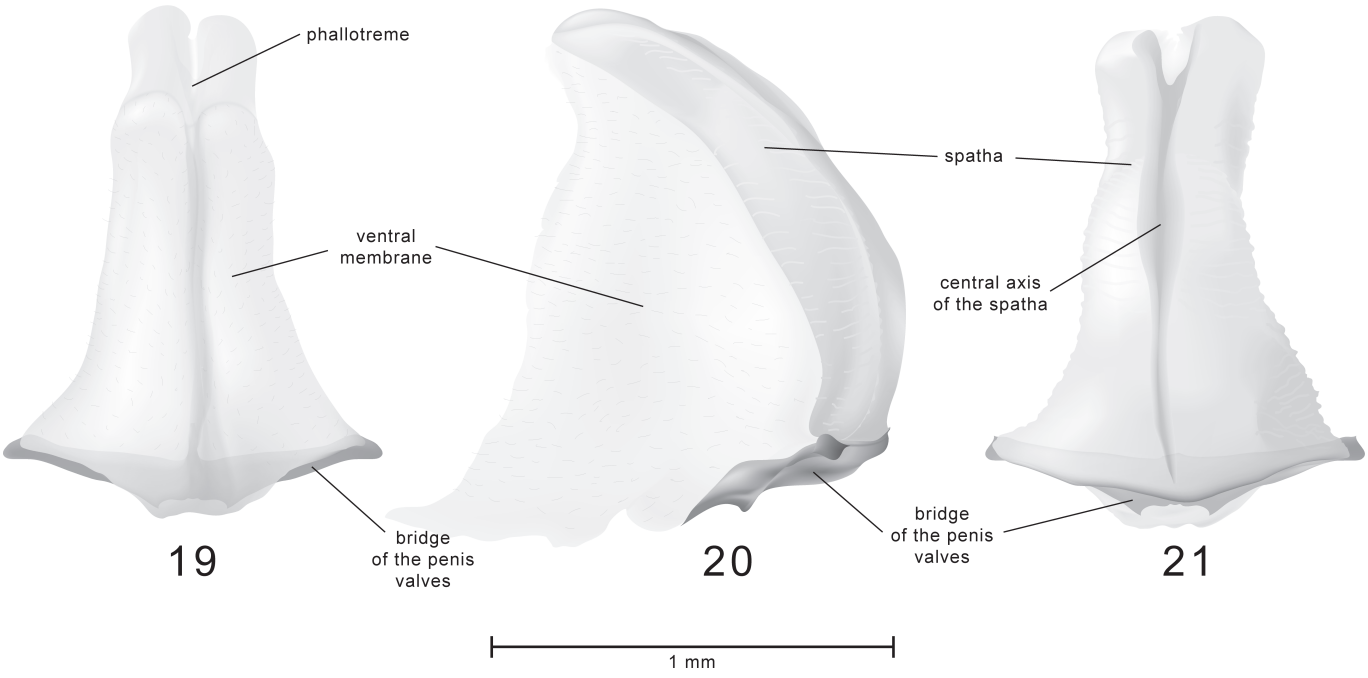
Figs. 16-18. *Euglossa imperialis,* penis valve. 16. Ventral view. 17. Lateral view. 18. Dorsal view.

a support for the penis as it forms a movable articulation with the bridge of the penis valves through the dorsal lamellae that run mesaly from the dorsum of the apodeme-base on each penis valve (Figs. 13-15).

The morphology of the penis valves is conserved in *Euglossa*. There is some slight variation in size and projection of the ventral blades. Moreover, some variation can be found in the shape of the posterior edge of the outer blade, which is more noticeably convex in groups like *Euglossella* and some *Glossurella*. The same edge on its dorsal extreme is conspicuously notched in *Euglossella* (e.g., Hinojosa-Díaz and Engel, 2007).

Eufriesea and *Eulaema* have penis valves composed of the same sections described for *Euglossa* although the whole structure seems to be more sclerotized, with less membranous interconnections. In both genera, the posterior edge of the outer blade is notched, as mentioned for *Euglossella*, but to a greater extent in some cases. The scoop-like modification of the posterior surface of the apodeme-base is exclusive of *Euglossa*, while in *Eufriesea* and *Eulaema* it is truncate, and convex in *Exaerete*. In *Eulaema*, in particular, the ventral blades are smaller and the dorsal section (although distinguishable) is fused to them. In *Exaerete* there is no definite dorsal section and the inner blade is rather small. *Aglae* has a completely different situation: both penis valves and the bridge of the penis valves are fused in a continuous, non-articulated structure with bulgy penis valves covered by dense, moderately-long setae on their outer surfaces (Kimsey, 1987). In *Bombus* the penis valves are less elaborate than in Euglossini, with smaller ventral projections, although with interesting modifications on their own (Ito, 1985). In Meliponini the penis valves are simple, hook-like projections. In Centridini there are several species groups in which the conformation of the penis valves is very similar to the one described for *Aglae*, although the bulgy ventral projections show different arrangements depending on the group, and in several of them also take sheath-like shapes. Similar situations are found in Anthophorini.

Penis.—The penis in *E. imperialis* is a saclike structure occupying a mesoposterior location in the genital capsule, between the penis valves by which it is supported. The base of the penis is formed by the bridge of the penis valves (Figs. 19-21). The bridge of the penis valves is a strong plate articulated to the penis valves through their dorsal lamellar projections. The structure of the bridge is built along three main sclerotic ridges, two of them expanding laterally to form the acute arms and a mesal one that continues dorsally as the main axis of the spatha (Figs. 20-21). Ventrally this bridge has two small acute projections that form a semicircular invagination. The whole dorsal edge of the bridge bends dorsally to form the convex spatha, which is a weaker sclerotic lamina narrowing apically, with a central axis (continuing from the mesal sclerotic ridge), slightly invaginated all along (Figs. 20-21). The lateral sections are strengthened by minor ridges perpendicular to the main axis. The apex of the spata is bilobed. Together the bridge of the penis valves and the spatha serve as the



Figs. 19-21. *Euglossa imperialis*, penis. 19. Ventral view. 20. Lateral view. 21. Dorsal view.

anterior and dorsal sclerotic supports of the membranous ventral surface of the penis. This ventral membrane is attached anteriorly to the membranes that close the inner open sections of the gonocoxites and to the posteromesal extremes of the basal section of the gonocoxite. Most of the membrane surface is covered with short setae. The phallotreme is located subapically between the bilobed apex of the spatha. (Figs. 19-21). According to Roig-Alsina (1993) the genus *Euglossa* has a simple, bag-like eversible endophallus with conspicuous spiculation, evidence of which can be seen in dissected genital capsules through the external membranous wall of the penis.

The penis variation in *Euglossa*, in taxonomic and systematic terms, can be seen in the relative length and width of the spatha, as well as in the extent of the central axis of the spatha. The spatha is evidently longer than its basal width in most species of *Euglossa sensu stricto*, all *Glossura*, most *Glossuropoda*, and some *Glossurella*, while the rest of the species have a spatha about as long as its basal width. *Euglossa sensu stricto*, *Glossura*, *Glossuropoda*, and some *Glossurella* have a complete central axis, slightly invaginated, as described for *E. imperialis*. Most other species have a non-invaginated central axis running only mid-distance to the apex of the penis. In *Euglossella* it is restricted to the very anterior extreme of the spatha (e.g., Hinojosa-Díaz and Engel, 2007). The axis is absent in *E. villosa*. In *Euglossella* the spatha is reinforced by small longitudinal wrinkles instead of the transverse ones present in most of the species.

In the other Euglossini, the bridge of the penis valves (either differentiated or fused) is oriented dorsally in the same plane as the spatha; this causes the two ventrally-oriented projections seen in *Euglossa* to be oriented anteriorly. The spatha is rather short, although wide in *Eufriesea* and *Eulaema*, short and narrow in *Aglae*, and practically absent in *Exaerete*. In none of these genera there is a noticeable central axis to the spatha. Kimsey (1987) mentioned the setose penis as a derived characer in *Euglossa* and in the other euglossine genera appearing asetose. However, on a closer examination, there seems to be setose areas in all Euglossini, very noticeable in *Aglae* and restricted to small ventral areas in the other genera. Setose penes are also easily identifiable in at least Centridini.

In *Bombus*, the bridge of the penis valves is rather different in shape to the one in Euglossini, while the spatha is narrow (in most species) and long (Ito, 1985). In Meliponini the spatha is wide. In Centridini, several groups have a very weak bridge of the penis valves, and the spatha is generally configured as in *Eufriesea* and *Eulaema*. In Anthophorini the bridge is well sclerotized and the spatha, likewise, similar to the aforementioned euglossines.

DISCUSSION

The immediately captivating external morphology of euglossine bees combined with the interesting suite of external secondary sexual characteristics of the males have served as the foundation for the taxonomy of the tribe. This situation is particularly evident for *Euglossa*, the largest genus of the tribe, in which the dominance of these characters has relegated to obscurity the use of other important sets of morphological features, notably the male genitalia and hidden metasomal sterna. As mentioned before, few species of *Euglossa* were described with references to the male genital structures; those original descriptions that include these features are mainly of new species described in the last two years (Parra-H *et al.*, 2006; Ramírez, 2006; Rasmussen and Skov, 2006; Hinojosa-Díaz and Engel, 2007). The traditionally used external characters are obviously useful, but there is no reason to ignore the important information contained in the genital capsule and the hidden metasomal sterna.

As detailed in the present work, the diversity of the different components of the genitalia and the hidden sterna in the genus *Euglossa* provides a considerable source of characters important in terms of recognition of species or species groups, but perhaps more significantly, as valuable added information to be applied in systematic and phylogenetic studies. A good example of this usage is the recently published phylogenetic study and revision of an assemblage within *Euglossa sensu stricto* (Bembé, 2007). The infrageneric categories in use for *Euglossa* (Cockerell, 1917; Moure, 1967, 1989; Dressler,1978b, 1982b, c, d), based exclusively on external morphology, are applicable without much trouble to a good number of species. However, there are instances in which the sole presence or absence of particular characters of the male make it hard to be certain of appropriate subgeneric assignment. The subgenus *Glossurella* is a clear example of a difficult assemblage of species that do not seem to be necessarily closer to one another than to other groups within the genus. For instance, the group of species allied to *E. allosticta*, all included in *Glossurella* (Dressler, 1982b), are externally very similar to bees in the subgenus *Glossura*, from which they differ by the lack of some structures (mesotibial tufts, sternal cowls) that are used for defining this subgenus. Upon reviewing the genital characters, it becomes clear that this assemblage belongs in *Glossura*. This can be seen in the depiction of the genital structures of *E. asarophora* and *E. rufipes* (Rasmussen and Skov, 2006), which are similar to those described here for *E. imperialis*, a member of *Glossura*. This situation is repeated for other

groups within *Glossurella*, only varying the characters involved. Another good example of troubled taxonomic status, with the exclusive use of non-genital external morphology, is that of *E. nigrosignata*, originally described in *Glossura* by Moure (1969), then moved to *Glossurella* by Dressler (1982b), and recently transferred to *Glossuropoda* by Roubik (2004). The male genitalia of *E. nigrosignata* reveal few similarities to those of *Glossura* or *Glossuropoda* since it poses a unique gonostylar morphology more similar to that of some species in *Glossurella*. There are more examples like these, which reveal the necessity of a revision of the present subgeneric classification of *Euglossa* (Hinojosa-Díaz, in prep.). Notwithstanding, the external characters used in the subgeneric classification define some well demarcated groupings inside *Euglossa*, such as *Euglossella* whose genital characters only reinforce the distinctivenes of this subgenus. With the current situation, it would be preferred to take a more conservative position, such as the one of Michener (2007) who prefers to place all the subgeneric names as synonyms under the name *Euglossa*. The outstanding secondary sexual characters of the males that heavily influence this classification are useful characters; however, their usefulness is limited if ignoring other sources of information that can help to solve the controversies created when such characters are unable to clearly resolve taxonomic status, and it is in this context where the characters from the genital structures enter to play their best role.

It is clear that a phylogenetic framework is needed to produce a more stable and reliable infrageneric partition of *Euglossa* and the main purpose of this study is to present a basis of the male genital morphology, in order to be included in an infrageneric phylogenetic analysis, based on morphology, currently in progress by the author, but also to provide a basis of comparative morphology of the structures here described, and to encourage their use.

LITERATURE CITED

Anjos-Silva, E. J. dos, and J. J. M. Rebêlo. 2006. A new species of *Exaerete* Hoffmannsegg (Hymenoptera: Apidae: Euglossini) from Brazil. Zootaxa 1105:27–35.

Anjos-Silva, E. J. dos, M. S. Engel, and S. R. Andena. 2007. Phylogeny of the cleptoparasitic bee genus *Exaerete* (Hymenoptera: Apidae). Apidologie 38:1–7.

Ayala B. R. 1998. Sistemática de los taxa supraespecificos de las abejas de la tribu Centridini (Hymenoptera: Anthophoridae). Doctoral Dissertation. México, D.F., México: Universidad Nacional Autónoma de México. iv + 280 pp.

Bembé, B. 2007. Revision der *Euglossa cordata*-Gruppe und Untersuchungen zur Funktionsmorphologie und Faunistik der Euglossini (Hymenopetra, Apidae). Entomofauna Zeitschrift für Entomologie 14:1–146.

Brooks, R. W. 1988. Systematics and phylogeny of the Anthophorine bees (Hymenoptera: Anthophoridae; Anthophorini). The University of Kansas Science Bulletin 53(9):436–575.

Camargo J. M. F., W. E. Kerr, and C. R. Lopes. 1967. Morfologia externa de *Melipona* (*Melipona*) *marginata* Lepeletier (Hymenoptera, Apoidea). Papéis Avulsos de Zoologia (São Paulo) 20(20):229–258. pls. A-P plus one unlettered.

Cockerell, T. D. A. 1917. Some euglossine bees. The Canadian Entomologist 49:144–146.

Cockerell, T. D. A. 1922. Bees in the collection of the United States National Museum. –4. Proceedings U.S. National Museum 60:1–20.

Dressler, R. L. 1978a. New species of *Euglossa* from Mexico and Central America. Revista de Biología Tropical 26(1):167–185.

Dressler, R. L. 1978b. An infrageneric classification of *Euglossa*, with notes on some features of special taxonomic importance (Hymenoptera: Apidae). Revista de Biología Tropical 26(1):187–198.

Dressler, R. L. 1982a. Biology of the orchid bees (Euglossini). Annual Review of Ecology and Systematics 13:373–394.

Dressler, R.L. 1982b. New species of *Euglossa*. II. (Hymenoptera: Apidae). Revista de Biología Tropical 30(2):121–129.

Dressler, R. L. 1982c. New species of *Euglossa*. III. The *bursigera* species group (Hymenoptera: Apidae). Revista de Biología Tropical 30(2):131–140.

Eickwort, G. C. 1969. A comparative morphological study and generic revision of the augochlorine bees (Hymenoptera: Halicitidae). University of Kansas Science Bulletin 48(13):325–524.

Engel, M. S. 1999. The first fossil *Euglossa* and a phylogeny of the Orchid Bees (Hymenoptera: Apidae; Euglossini). American Museum Novitates 3272:1–14.

Engel, M. S. 2007. A lateral gynandromorph in the bee genus *Thyreus* and the sting mechanism in the Melectini (Hymenoptera: Apidae). American Museum Novitates 3553:1–11.

Hinojosa-Díaz, I. A. and M. S. Engel. 2007. Two new orchid bees of the subgenus *Euglossella* from Peru (Hymenoptera: Apidae). Beiträge zur Entomologie 57:93–104.

Ito, M. 1985. Supraspecific classification of bumblebees based on the characters of male genitalia. Contributions from the Institute of Low Temperature Science, Hokkaido University Series B(20):1–143.

Kimsey, L. S.1979. An illustrated key to the genus *Exaerete* with descriptions of male genitalia and biology (Hymenoptera: Eglossini, Apidae). Journal of the Kansas Entomological Society 52(4):735–746.

Kimsey, L.S. 1982. Systematics of bees of the genus *Eufriesea*. University of California Publications in Entomology 95:i–ix + 1–125.

Kimsey, L. S. 1987. Generic relationships within the Euglossini (Hymenoptera: Apidae). Systematic Entomology 12:63–72.

Michener, C. D. 1944a. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bulletin of the American Museum of Natural History 82:151–326.

Michener, C. D. 1944b. A comparative study of the appendages of the eighth and ninth abdominal segments of insects. Annals of the Entomological Society of America 37:336–351.

Michener, C. D. 1956. Hymenoptera, pp. 131-140,. in Tuxen, S. L. (ed.): Taxonomist's Glossary of Genitalia in Insects. Copenhagen: Ejnar Munksgaard.

Michener, C. D. 1990. Classification of the Apidae. University of Kansas Science Bulletin 54:75–153.

Michener, C. D. 2007. The Bees of the World [2nd Edition]. Baltimore, MD: Johns Hopkins University Press. xvi + [1] + 953 pp.

Moure, J. S. 1967. A check-list of the known euglossine bees (Hymenoptera, Apidae). Atas do Simpósio sôbre a Biota Amazônica 5(Zoologia):395–415.

Moure J. S. 1969. The Central American species of *Euglossa* subgenus *Glossura* Cockerell, 1917 (Hymenoptera, Apidae). Revista de Biología Tropical 15:227–247.

Moure, J. S. 1989. *Glossuropoda*, novo subgênero de *Euglossa*, e duas

espécies novas da Amazônia, do mesmo subgênero (Apidae - Hymenoptera). Memórias do Instituto Oswaldo Cruz 4:387–389.
Oliveira, M. L. de. 2006. Nova hipótese de relacionamento filogenético entre os gêneros de Euglossini e entre as espécies de *Eulaema* Lepeletier, 1841 (Hymenoptera: Apidae: Euglossini). Acta Amazonica 36(2):273–286
Ospina-Torres, R., A. Parra-H, and V. H. Gonzalez. 2006. The male gonostylus of the orchid bee genus *Euglossa* (Apidae: Euglossini). Zootaxa 1320:49–55
Parra-H, A., R. Ospina-Torres, and S. Ramírez. 2006. *Euglossa natesi* n. sp., a new species of orchid bee from the Chocó region of Colombia and Ecuador (Hymenoptera: Apidae). Zootaxa 1298:29–36
Ramírez, S., R. L. Dressler, and M. Ospina. 2002. Abejas euglosinas (Hymenoptera: Apidae) de la Región Neotropical: listado de especies con notas sobre su biología. Biota Colombiana 3(1):7–118.
Ramírez, S. 2006. *Euglossa samperi* n. sp., a new species of orchid bee from the the Ecuadorian Andes (Hymenoptera: Apidae). Zootaxa 1272:61–68.
Rasmussen, C. and C. Skov. 2006. Description of a new species of *Euglossa* (Hymenoptera: Apidae: Euglossini) with notes on comparative biology. Zootaxa 1210:53–67.
Rebêlo, J. M. M. 2001. História Natural das Euglossineas, as Abelhas das Orquídeas. São Luís, Brasil: Lithograf Editora. 152 pp.
Roig-Alsina, A. 1993. The evolution of the apoid endophallus, its phylogenetic implications, and functional significance of the genital capsule. Bollettino di Zoologia 60:169–183
Roubik, D. W. 2004. Sibling species of *Glossura* and *Glossuropoda* in the Amazon Region (Hymenoptera: Apidae: Euglossini). Journal of the Kansas Entomological Society 77(3):235–253.
Roubik, D. W., and P. E. Hanson. 2004. Orchid bees of tropical America, biology and field guide. Santo Domingo de Heredia, Costa Rica: Instituto Nacional de Biodiversidad, INBio. 352 pp.
Rozen, J. G. 1951. A preliminary comparative study of the male genitalia of Andrenidae (Hymenoptera, Apoidea). Journal of the Kansas Entomological Society 24(4):142–150.
Schulmeister, S. 2001. Functional morphology of the male genitalia and copulation in lower Hymenoptera, with special emphasis on the Tenthredinoidea s. str. (Insecta, Hymenoptera, "Symphyta"). Acta Zoologica (Stockholm) 82:331–349.

APPENDIX

Species studied by direct examination of dissected specimens:

E. (*Dasystilbe*) villosa Moure

E. (*Euglossella*) *bigibba* Dressler
E. (*Euglossella*) *cosmodora* Hinojosa-Díaz & Engel
E. (*Euglossella*) *cyanea* Friese
E. (*Euglossella*) *cyanura* Cockerell
E. (*Euglossella*) *decorata* F. Smith
E. (*Euglossella*) *granti* Cheesman
E. (*Euglossella*) *mandibularis* Friese
E. (*Euglossella*) *perpulchra* Moure & Schlindwein
E. (*Euglossella*) *perviridis* Dressler
E. (*Euglossella*) *polita* Ducke
E. (*Euglossella*) *viridis* (Perty)

E. (*Glossurella*) *allosticta* Moure
E. (*Glossurella*) *asarophora* Moure
E. (*Glossurella*) *augaspis* Dressler
E. (*Glossurella*) *bursigera* Moure
E. (*Glossurella*) *dodsoni* Moure
E. (*Glossurella*) *gorgonensis* Cheesman
E. (*Glossurella*) *hyacinthina* Dressler
E. (*Glossurella*) *laevicincta* Dressler
E. (*Glossurella*) *macrorhyncha* Dressler
E. (*Glossurella*) *nigrosignata* Moure
E. (*Glossurella*) *obtusa* Dressler
E. (*Glossurella*) *oleolucens* Dressler
E. (*Glossurella*) *parvula* Dressler
E. (*Glossurella*) *sapphirina* Moure
E. (*Glossurella*) *stilbonota* Dressler
E. (*Glossurella*) *turbinifex* Dressler
E. (*Glossurella*) *viridifrons* Dressler

E. (*Glossura*) *annectans* Dressler
E. (*Glossura*) *imperialis* Cockerell
E. (*Glossura*) *piliventris* Guérin
E. (*Glossura*) *stellfeldi* Moure

E. (*Glossuropoda*) *intersecta* Latreille
E. (*Glossuropoda*) *rugilabris* Moure

E. (*Euglossa*) *cognata* Moure
E. (*Euglossa*) *cordata* (Linnaeus)
E. (*Euglossa*) *cybelia* Moure
E. (*Euglossa*) *deceptrix* Moure
E. (*Euglossa*) *hansoni* Moure
E. (*Euglossa*) *iopyrrha* Dressler
E. (*Euglossa*) *mixta* Friese
E. (*Euglossa*) *nigropilosa* Moure
E. (*Euglossa*) *townsendi* Cockerell
E. (*Euglossa*) *tridentata* Moure
E. (*Euglossa*) *viridissima* Friese

Aglae caerulea Lepeletier de Saint Fargeau & Audinet-Serville
Eufriesea caerulescens (Lepeletier de Saint Fargeau)
Eufriesea auripes Gribodo
Eulaema polychroma (Mocsáry)
Eulaema speciosa (Mocsáry)
Exaerete smaragdina (Guérin-Méneville)
Exaerete frontalis (Guérin-Méneville)

Bombus sp.
Anthophora dufourii Lepeletier de Saint Fargeau
Centris birkmanii Friese
Centris poecila Lepeletier de Saint Fargeau
Centris labrosa Friese
Epicharis metatarsalis Friese

Taxa for which literature was consulted (for each work cited, all species depicted were used for comparative statements in this study):

Eufriesea spp. (Kimsey, 1982)
Eulaema spp. (Oliveira, 2006)
Exaerete spp. (Kimsey, 1979)
Bombus spp. (Ito, 1985; Michener, 1990, 2007)
Anthophora spp. (Brooks, 1988)
Centridini spp. (Ayala, 1998)

PUBLICATIONS OF THE NATURAL HISTORY MUSEUM, THE UNIVERSITY OF KANSAS

The University of Kansas Publications, Museum of Natural History, beginning with Volume 1 in 1946, was discontinued with Volume 20 in 1971. Shorter research papers formerly published in the above series were published as The University of Kansas Natural History Museum Occasional Papers until Number 180 in December 1996. The Miscellaneous Publications of The University of Kansas Natural History Museum began with Number 1 in 1946 and ended with Number 68 in February 1996. Monographs of The University of Kansas Natural History Museum were initiated in 1970 and discontinued with Number 8 in 1992. The University of Kansas Science Bulletin, beginning with Volume 1 in 1902, was discontinued with Volume 55 in 1996. The foregoing publication series are now combined in a new series entitled Scientific Papers, Natural History Museum, The University of Kansas, begun with Number 1 in 1997. Special Publications began in 1976 and continue as an outlet for longer contributions and are available by purchase only. All manuscripts are subject to critical review by intra- and extramural specialists; final acceptance is at the discretion of the editor.

The publication is printed on acid-free paper. Publications are composed using Microsoft Word® and Adobe InDesign® on a Macintosh computer and are digitally printed through Allen Press, Inc., Lawrence, Kansas.

Available back issues of The University of Kansas Science Bulletin may be purchased from the Library Sales Section, Retrieval Services Department, The University of Kansas Libraries, Lawrence, Kansas 66045-2800, USA. Available issues of former publication series, Scientific Papers, and Special Publications of the Natural History Museum can be purchased from the Office of Publications, Natural History Museum, The University of Kansas, Lawrence, Kansas 66045-2454, USA. Purchasing information can be obtained by calling (785) 864-4450, fax (785) 864-5335, or e-mail (kunhm@ukans.edu). VISA and MasterCard accepted; include expiration date.

SERIES EDITOR: Kirsten Jensen

PRINTED BY
ALLEN PRESS, INC.
LAWRENCE, KANSAS